Analysing livestock network data for infectious diseases control

Analysing livestock network data for infectious diseases control: an argument for routine data collection in emerging economies

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Abstract

Livestock movements are an important mechanism of infectious disease transmission. Where these are well recorded, network analysis tools have been used to successfully identify system properties, highlight vulnerabilities to transmission and inform targeted surveillance and control. Here we highlight the main uses of network properties in understanding livestock disease epidemiology, discuss statistical approaches to infer network characteristics from biased or fragmented datasets. We use a "hurdle model" approach that predicts (i) the probability of movement and (ii) the number of livestock moved to generate synthetic 'complete' networks of movements between administrative wards, exploiting routinely collected government movement permit data from northern Tanzania. We demonstrate that this model captures a significant amount of the observed variation. Combining the cattle movement network with a spatial between-ward contact layer we create a multiplex, over which we simulated the spread of 'fast' (R_0=3) and 'slow' (R_0=1.5) pathogens, and assess the effects of random versus targeted disease control interventions (vaccination and movement ban). The targeted interventions substantially outperform those randomly implemented for both fast and slow pathogens. Our findings provide

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motivation to encourage routine collection and centralisation of movement data to construct representative networks.

1. Introduction

The "static network" concept of a population as a set of "individuals" (nodes) with immutable contacts (links) between them is now well-established in infectious disease modelling. The network representation occurs naturally because the "individual" is typically well-defined (e.g. a person, animal, city, herd, or farm) and the number of potentially infectious contacts per individual is usually few [1-5]. While there are a few studies for human diseases that include comprehensive, explicit network data [6], more frequently these are either generated indirectly (for example, using mobile phone data or gravity models to predict commuter flow [7-10]), or are explicit but at small geographical scales [11, 12]. In contrast, in Great Britain (GB) cattle movement data have been recorded for individuals on a daily basis for almost two decades [13]. This data richness has presented both challenges and opportunities for the application of network analyses in infectious disease epidemiology [4, 5]. Similar livestock data now exist in many other countries [14-20]. However, they remain rare in emergent economies where disease burden is often high and zoonotic risk is more pronounced due to the high proportion of people who live and work in close contact with livestock [21]. About one billion of the world's poorest people (earning < US$2 per day) depend at least partially on livestock for their livelihoods [22], making the trade of livestock and the freedom to move livestock to access natural resources vital in many impoverished communities [23-25]. In many regions, such as Sub-Saharan Africa, there are frequent but poorly recorded cross-border movements [26-28] and, when coupled with poor within-country knowledge of livestock movements, this creates risks for international pathogen transmission.

Though network analyses would be greatly aided by systems for comprehensive routine recording of between-farm and market movement, as occurs in GB and elsewhere, in countries with developing infrastructure collecting these data can be onerous and costly and requires well-evidenced justification. Here, we provide an overview of the role of network analysis in epidemiology, paying particular

attention to the challenges of exploiting extensive but fragmented data. These insights are used to analyse livestock movements in northern Tanzania, where there is a high burden of livestock disease including zoonoses [29-35], no formal livestock traceability system implemented at a national level, and limited resources for disease control. We demonstrate the utility of our network by identifying nodes to target disease control and surveillance interventions, considering both fast and slowly transmitting pathogens, and interrogate their efficacy through simulation, demonstrating substantial potential benefits in reducing disease spread.

2. Fundamental network concepts applied to livestock diseases

2.1 Centrality measures and transmission patterns

Network centrality measures originated in social science [36], and are used to quantify the importance of nodes and links in a network, with obvious applications to identifying disease risks [19, 37-41]. Common measures include degree centrality (the number of links associated with a node[a]), betweenness centrality (the number of times a node or link is traversed by the shortest paths between all other node pairs), and eigenvector centrality (loosely, a measure of how connected a node is to well-connected neighbours).[b] Network centrality measures have been used to analyse livestock movement data from many countries, with each using different types of data source [4, 17, 40-43]. One example showing the relevance of all three of these centrality measures comes from the analysis of the costly [44] 2001 foot-and-mouth disease (FMD) epidemic in GB. First, a small number of "cull ewes" were sold and transported long distance across GB; these were responsible for seeding virus into many otherwise low risk areas [45]. These seeding movements are a characteristic of "small world" network behaviour [1] with the long-range movements acting as links with high betweenness centrality [45, 46]. Second, Longtown auction market (the largest in GB) played a dominant role in spreading disease [47], demonstrating the importance of high degree centrality. Third, since the epidemic, prohibition of direct

[a] For directed networks like livestock movements, where transmission is overwhelmingly in the direction of the movement only, the geometric mean of in- and out-degree can be used.

[b] See the supplementary information for a disease-relevant interpretation.

82 market-to-market livestock movements means that some farms now act as "middlemen" between
83 markets, representing a risk that could be effectively targeted to restrict disease spread [4, 48]. This
84 role, linking highly connected nodes, is a well-recognised feature of high eigenvector centrality.
85
86 **2.2. Network Dynamics**
87
88 In a static network, the infection pressure from a single individual is reduced over time as each daughter
89 infection 'uses up' the link it was infected over [49, 50]. Further, the components of the network (groups
90 of nodes which can reach each other) are well defined. In dynamic networks, links can shift between
91 individuals over time (rewiring), nodes can appear or disappear and the components of the network can
92 change in size and composition. Rewiring a link away from an infected individual has the potential to
93 expose another susceptible individual, thus increasing the probability of disease persistence [51, 52].
94 Link dynamics also greatly complicate measures of network structure. For example, for an *SIS* infection
95 process on a static network, where susceptible individuals (*S*) can become infected (*I*) and eventually
96 recover to susceptible again, the eigenvector centrality scores of the nodes of the network contact matrix
97 represents the expected proportion of time those nodes are infected over the long term[a]. This is the case
98 so long as the probability of recovery before re-infection is high (e.g. if the density of infected nodes is
99 always low, or the recovery time is substantially shorter than the time between infected generations).
100 However, livestock movements vary daily, seasonally and from year-to-year. Contact patterns between
101 farms and therefore eigenvector centrality measures can change dramatically depending on the season
102 and stochastic progression of the epidemic. This influences epidemic spread [4, 13, 18, 51], an effect
103 also seen in human diseases [14, 53]. Individual variability in disease progression and severity will
104 also influence disease generation times and therefore what movements are likely to cause infection
105 spread. Thus, predictions of node importance and targeting can depend strongly both on the dynamic

[a] For an irreducible positive definite matrix (e.g. a contact matrix where all nodes belong to a single strong component), the Perron-Frobenius theorem applies and the matrix is guaranteed to have a unique largest eigenvalue (and positive eigenvector). For directed networks, strong connectivity amongst all nodes is required (all nodes can reach each other reciprocally, i.e. are members of the same strong component). Where this is not the case, eigenvector centrality is not well-defined, and other network measures need to be considered (for example by using singular values).

properties of the network and the properties of the underlying disease, making the identification of general principles for the targeting of control more challenging (e.g. [54]; also Supplementary Information).

Livestock movements are also an example where the actual contact occurs episodically. Episodic behaviour is a subject of considerable study in the network literature, especially where there are patterns of concentrated bursts ("burstiness") separated by long waiting periods [55-57]. While an infection may itself cause episodic activity, it is most frequently studied as a property of the underlying network. Episodic activity has been shown to slow an epidemic on simulated [58] and real networks [59] but can also increase epidemic speed, for example, due to observed correlations between the topology of the network and the frequency of episodic contacts [60]. Epidemic spread also depends on within-node infection dynamics; in a simulated avian influenza outbreak, patterns of recorded vehicle movement between farms could either slow or accelerate pathogen spread, depending on the disease parameters and detection threshold at the farm level [61].

Infection events themselves can also change the network structure. If the perceived jeopardy is sufficiently high, rumours of pathogen spread may change contact patterns [62, 63]. For livestock, farmers may be inclined to sell infected animals due to their condition, or may be restricted from selling animals until the farm is officially declared disease-free [64]. In human disease, modelling analyses that included changes in the contact process over the course of the recent West African Ebola epidemic were used to inform changes in policy [65], highlighting the relevance for detailed datasets on contact patterns and their changes over time, both routinely and in response to an outbreak [66].

2.3 The role of pathogen sequence data for relating transmission networks to livestock networks

Although livestock movements tell us about potentially infectious contacts, the relationship between these contacts and the transmission network of actual infectious contacts is only partially understood. Duration of contact, heterogeneity in immune response, and environmental conditions are some of the

134 factors that could affect which livestock movements transmit infection. The growing availability of high
135 coverage pathogen sequence data provides an unprecedented opportunity to quantify this relationship
136 [67, 68]. A number of tools have been developed to estimate transmission from genetic data [69-78]
137 and new tools continue to be developed [69, 73, 79]. However there remain many challenges [80-84].
138 A key limitation is that pathogen evolution needs to occur on a similar or faster timescale to the disease
139 generation time in order to infer direction of transmission [80]. Considering larger epidemiological units
140 (e.g. farms rather than animals) can alleviate this problem, since the generation time will be
141 concomitantly longer [73, 74, 77]. Epidemiological information is still required to estimate transmission
142 from genetic data and contact network data is important when trying to identify the most likely
143 transmission events [85, 86], but there are few tools to formally integrate these [87]. Phylodynamic
144 approaches that leverage all available data could provide new insights into pathogen transmission and
145 result in more targeted and improved control interventions, but they must overcome the challenge of
146 appropriate weighting of the often biased and/or fragmented data. Nevertheless, even limited genetic
147 data integrated into transmission models can improve epidemiological insights [88] and in situations
148 where other data are fragmented or sparse, sequence data can greatly strengthen the understanding of
149 transmission and inform control.
150
151 **Section 3. Exploiting network properties**
152
153 **3.1. Evaluating system resilience**
154
155 Invasion of a livestock network by an infectious pathogen has the capacity to impair or destroy the
156 function of individual nodes, either by the direct impact on livestock, or by the restrictions resulting
157 from control efforts. The impact on network structure can be considerable, *in extremis* resulting in the
158 destruction of the network as a functioning entity. For infectious diseases, interventions such as
159 movement restrictions, culling or prolonged herd testing are all designed to reduce transmission, but
160 will also have varying degrees of impact on livestock movements and potentially impair the nodes role
161 in the network. Such changes have economic impact [89, 90] and, if sufficiently harmful, can result in

node removal and/or substantial long-term harm to the network. Resilience of a network typically focuses on its ability to recover, retain the same structure, and adapt to maintain system functionality when exposed to disturbances [91-93]. One approach to eliminate disease, such as during the 2001 FMD epidemic, is to disrupt the network by preventing trade for a period (link removal). These movement restrictions, however, can result in excessive livestock welfare issues, welfare culls, and significant long term industry damage [94]. Less disruptively, lasting adjustments (link rewiring) can minimize the impact of highly influential nodes, whilst maintaining overall trade function. An example of this is the implementation of high biosecurity and compartmentalisation in some poultry companies to isolate themselves from disease incursion despite close physical proximity to infected farms, allowing operations to continue in the face of national restrictions [95].

Minimising the number of affected nodes, or protecting particular ones, may be important for resilience. In dynamic networks, slowing the rate at which contacts occur can slow the rate of pathogen spread and maintain communication between nodes [4], improving the networks resilience. Conversely, reducing contact rates can also increase pathogen spread [61]. Additional complications arise when considering multiple layers of a network and multiple diseases that spread on it. Ultimately, targeting control measures that consider the spread of multiple pathogens on a network could be more efficient and robust. Additionally, prior to designing and imposing changes on a network, particularly in economies where livelihoods are heavily dependent on a functioning livestock movement network, the network's resilience to proposed changes should assessed.

3.2. Exploiting network data to improve surveillance

The concepts of network resilience can be used to improve surveillance. Albert *et al.* showed the extent to which different types of complex network can be resilient to breakdown (which makes disease difficult to control) or vulnerable to breakdown (which makes disease easier to control) [96]. Nodes (or links) can be removed from a network randomly or using targeted measures such as removing nodes that are highly ranked by one or more centrality measure. In terms of surveillance, random and targeted

node removal can be compared to non-targeted and targeted surveillance [4]. Network analysis can thus provide an analytical framework to predict which farms to test in targeted surveillance strategies and estimate net gains in performance. While generic network analysis can be valuable [5], it can be made more robust by an understanding of the characteristics of the real system [97] and the dynamics of the considered pathogen [48]. Network analysis has been used to inform targeted surveillance strategies in many livestock systems [43, 97-100], leading to considerable gains in surveillance efficiency [101, 102]. Analyses of GB livestock networks have identified highly connected premises with a high risk of both becoming infected with and spreading disease [38], and have used simulations to show how targeted surveillance could reduce the size of potential epidemics [4]. For Swedish cattle and pigs, a bespoke metric was identified to consider the timing and sequence of possible incoming and outgoing infection chains [14]. This metric was subsequently expanded to consider the size of the in- and out-components and then used to analyse the German pig trade movements network to identify high-risk farms [15]. Such data are not typically available in low resource settings; having such network knowledge could enable the use of cost-efficient, network measure-targeted surveillance for disease control, but needs justification for the additional cost and effort required.

3.3. Multiplexes, multi-layer networks and multi-host pathogen systems

Complex systems are inherently multi-dimensional, with components linked via a complex set of often directed and weighted interactions, giving rise to diverse and unpredictable behaviours [103]. For infectious diseases, these can arise when spread occurs by more than one mechanism (e.g. animal trade, airborne, fomites, sharing a resource or insect vectors), resulting in a multiplex, or where transmission occurs across more than one species, an example of a multi-layer network. Both can compromise disease control [104], especially when there are biases in available data or ability to exert control [105]. The multiplex representation was first developed in the social sciences to represent different types of inter-personal relationships [106]. It has since been used in a variety of contexts, including ecological systems [107], air transport [108], behavioural biology [109], and epidemiology [110]. In one livestock example, a study of a dairy system in northern Italy explicitly accounted for two independent

transmission routes: cattle and veterinarian movements. This study found that at the local scale veterinarian movements explained the spread of *Mycobacterium avium* subspecies *paratuberculosis* better than cattle movements and geographic distance failed to capture the impact of veterinarian visits [111, 112]. This highlights a need to identify the potentially multiple transmission routes beyond discrete livestock movements when collecting data to construct a livestock network that is representative of a transmission network.

Many pathogens are multi-host and therefore the network multi-layer. This complication often has severe implications for humans, livestock and wildlife [113]. Unfortunately most analytical frameworks of resilience are unsuitable for multi-dimensional systems [114], and network resilience can be influenced by interdependence with other networks [115]. Recent work using percolation theory to study the vulnerability of a system of interdependent networks [116] shows the overlap between network layers can improve network resilience and this makes diseases harder to eradicate [117]. By disentangling system dynamics from system structure, network characteristics can be identified that influence resilience [115]. A well-known exemplar is the transmission of *Mycobacterium bovis*, the cause of bovine tuberculosis (bTB), between cows and European badgers (*Meles meles*), where the role of different layers can be quantified by exploiting their spatial patterns (Figure S1) [64]. At finer granularities, radio-collar data were used to quantify inter- and intra-species contacts for cattle and badgers [118]; adding a layer of indirect contacts based on badger latrines locations to this network showed better correspondence to badger-to-badger transmission patterns [119].

4. Movement networks where there is limited resource for explicit traceability

There are many examples where livestock movement data have facilitated the planning of disease control and surveillance [42, 120, 121][17, 19, 122]. Conversely, an absence of movement information can obstruct disease control [45, 123]. In settings where comprehensive tracing systems are absent, a variety of methods have been used to quantify livestock movement patterns and construct movement networks. These include the use of GPS collar data to describe mobility patterns of pastoral herds and

245 overlaps with wildlife areas [27, 43, 124, 125], household and market surveys [126], transport vehicle
246 records [127] and international movement permits [28, 128].
247
248 Movement permits are used in many countries to certify livestock health and/or to regulate movement
249 taxes, and have been used to quantify livestock flow and construct movement networks [128, 129]. The
250 often ephemeral and patchy nature of these records, due to poor archiving or non-compliance [130], can
251 results in substantial non-random "missingness" that is difficult to quantify. In these cases, movement
252 permits have been used in conjunction with household and/or market survey data to estimate the risk of
253 disease introduction and target surveillance and vaccination campaigns, also illustrating the importance
254 of a regional disease control approach [28, 122, 131, 132]. Such analyses have identified traders as key
255 targets for disease control [130], demonstrated the effects of cattle movement on regional disease
256 transmission [133], identified increased risks of bTB with increased herd introductions [41] and, with
257 serology data, identified the role of between-village cattle movements in transmitting Rift Valley fever
258 virus [134].
259
260 Biased network samples can make reconstruction of network characteristics difficult. This was
261 addressed in GB by extrapolating from a small biased network sample via statistical associations
262 between common factors in the network study and a national population survey [135].
263
264 Another approach to network construction is to impose an underlying model on observed population
265 densities. Specifically, if census data (populations and locations) are available or can be estimated,
266 gravity [136] and radiation [137] models provide two ways of creating network models of population
267 mobility. While there is ongoing research regarding their relative merits [138], they share the property
268 of describing movement in terms of relative population size and a measure of distance. Gravity models,
269 for example, describe the probability of a movement occurring in inverse proportion to spatial distance
270 from each hub.
271
272 **Section 5. Evaluating network-based control strategies for livestock movements in Tanzania.**

Introduction to the study

Tanzania provides an exemplar of a rapidly developing emerging economy. In northern Tanzania there is a heavy reliance upon livestock for food, traction power, income, savings and social status. Movements can be over long distances, often on foot, and occasionally over international boundaries with multiple levels of market activity [26, 85, 139, 140]. The pathogen burden is often high, and this impacts productivity, creates herd/flock instability and, in the case of zoonoses, directly affects human health [30, 32, 33, 141-146]. In addition to protecting human health, reducing the burden of endemic livestock pathogens to improve livestock health and productivity is recognised as a route away from poverty and necessary to meet global food demands [23, 147-153]. Livestock sales are also a major source of income in rural communities [154-156]. In addition to trade between markets, livestock can be sold privately, borrowed or gifted between households and are regularly moved to access natural resources [41, 157, 158]. A reduction in endemic livestock disease is therefore paramount to improving livelihoods in such emerging economies.

Historically there has been no formal, centralised system for identifying and tracing the movement of individual animals in Tanzania, however a paper movement permit certifying livestock health is officially required whenever animals are traded, recording movements *from* markets, though not movements *to* markets. These data are not digitised and the receipt books are stored at administrative Zonal Veterinary Centres in Tanzania. The aims of this study were to: quantify cattle and small ruminant movements in a large (97000 km^2) area of northern Tanzania (Arusha, Manyara and Kilimanjaro regions) using archived, routinely collected government movement permit data; infer livestock movement networks; and build this information into livestock disease simulations to inform surveillance and control.

Methods

Summary methods are presented here; for full details see the supplementary material.

Data source and transcription

301 Access was granted to archived government movement permit receipt books at the Northern Zonal
302 Veterinary Office, Arusha. Movement permit receipt books were selected for analysis from 2009, 2011,
303 2013 and 2015. Origin, destination, number of each species (cattle, sheep or goat) moved, and date were
304 manually entered into spreadsheets from 50% of the available permits (30,946 permits), of which
305 19,438 (63%) permits yielded complete data. Only cattle movements are analysed here.
306
307 Statistical Modelling
308 Cattle movements were aggregated temporally by month and spatially at the ward level, because origins
309 and destinations often could not be located at a finer scale. A ward is an administrative unit of mean
310 area 243 km^2 and mean human population of 12,000 across the 398 wards in the study regions [159].
311 We aimed to infer the inter-ward cattle movement network within the study area; movements to outside
312 the study area and within wards were excluded (local movements from markets are less likely to
313 generate a movement permit due to non-compliance). The resulting data set recorded the movement of
314 86,195 cattle from 98 origin wards to 239 destination wards over the 4 sampled years.
315
316 Due to the large number of non-randomly missing permits, it was not possible to use the movement
317 data directly. Instead, the network was inferred by statistical modelling of the observed movements.
318 First, to distinguish true from artefactual absence of movements (months where an origin ward sent out
319 no cattle) a zero-inflated negative binomial (ZINB) generalised linear model (GLM) was fitted to each
320 origin ward, so that in subsequent modelling steps movements would be imputed in place of false
321 zeroes. Next, inter-ward livestock movement was modelled using a hurdle model. The movement
322 between each pair of wards in a given month is represented by a two-step processes: the binary event
323 of any cattle being moved, modelled by a binomial generalised linear mixed-effects model (GLMM);
324 and the number of animals moved, modelled by a zero-truncated negative binomial (ZTNB) GLMM.
325 Each part of the hurdle model allowed movement to depend multiplicatively on the distance between
326 origin and destination wards and their "masses" (human and cattle population sizes), in addition to other
327 characteristics (Table S1). The combined models can therefore be viewed as a gravity model of the

328 livestock movement network. Unexplained spatial and temporal variation was modelled by fitting
329 random effects for origin and destination ward and for the 48 months.
330
331 Simulated networks
332 The fitted model was used to simulate monthly movements amongst the 398 wards for one year, with
333 the number of movements inflated twofold to account for using a 50% subsample of the data.
334
335 Network measures
336 The simulated data were used to create an observed year-aggregated, static, directed, weighted cattle
337 movement network. A spatial contact layer, connecting all adjacent wards, was added to the market
338 movements network as a simplified means of accounting for contacts and movements between wards
339 that are not represented by the movement permit data. Social network analysis was applied to the
340 resulting multiplex network to identify nodes with high in-degree, out-degree, betweenness and
341 eigenvector centrality where disease control interventions could be targeted.
342 Simulating disease outbreaks and control on the network
343 The spread of a 'fast' ($R_0 = 3$) and 'slow' ($R_0 = 1.5$) pathogen was simulated on the multiplex to assess
344 the effects of disease control interventions on the spread of pathogens with varying infectiousness [166].
345 This was achieved by running a stochastic *SIR* compartmental model within each ward. The total
346 number of cattle in the susceptible (*S*), infectious (*I*) and recovered (*R*) compartments was updated
347 daily, while cattle were moved monthly between wards. The two sources of simulated cattle movement
348 were long distance movements via the market network and short distance movements between adjacent
349 wards to account for unobserved local movements (for a full description see Supplementary
350 Information; an animation of a simulated fast epidemic is available as a supplementary file). Two types
351 of intervention were trialled: proactive vaccination of 70% of the cattle in a ward before the start of the
352 epidemic, and a reactive ban on cattle movements one month after the start of the epidemic. Vaccine
353 interventions were applied to all wards, or targeted at 20 (5%) of wards that were selected randomly,
354 based on their total cattle population size or based on their network centrality measures. The network
355 centrality measures used for targeting interventions were betweenness centrality, eigenvector centrality,

and geometric mean degree. The market movement ban was either implemented in all 111 wards that generated outward cattle movements in the simulations and were therefore assumed to have a market, or were targeted in a subset of 20 of these wards, the same number as in the targeted vaccination interventions, and based on the same selection criteria.

Results

The two parts of the hurdle model explained a substantial proportion (binomial: 40%; ZTNB: 24%) of the spatial and temporal variation in cattle movement, with movement being more probable over shorter distances and into wards containing a secondary market, and the number of animals moved being most strongly associated with the agro-ecological system of the origin wards and the presence of a primary or secondary market in the origin or destination ward (Table S1; Figure S2). All variables were retained in the hurdle model that was used to simulate the monthly cattle market movements.

Network and node measures

The multiplex network is fully strongly connected (all wards can be reached by all other wards) and displays 'small world' properties. The spatial network layer connects all adjacent wards and the permit-related movements reduce the network diameter (longest path length between two wards) from 18 on the spatial network to 12 (see supplementary material Table S2 for cattle market, spatial and multiplex networks summary statistics).

The distributions of the three node centrality measures that were investigated (betweenness, eigenvector, and geometric mean degree) were strongly right-skewed. This indicates that the multiplex may be sensitive to targeted disease control interventions at the highly influential nodes. Figure 1 shows the geographical distribution of the top-ranked wards for each centrality measure, showing the potential for substantial differences in the effectiveness of targeting controls based on centrality measures due to their geographical distribution.

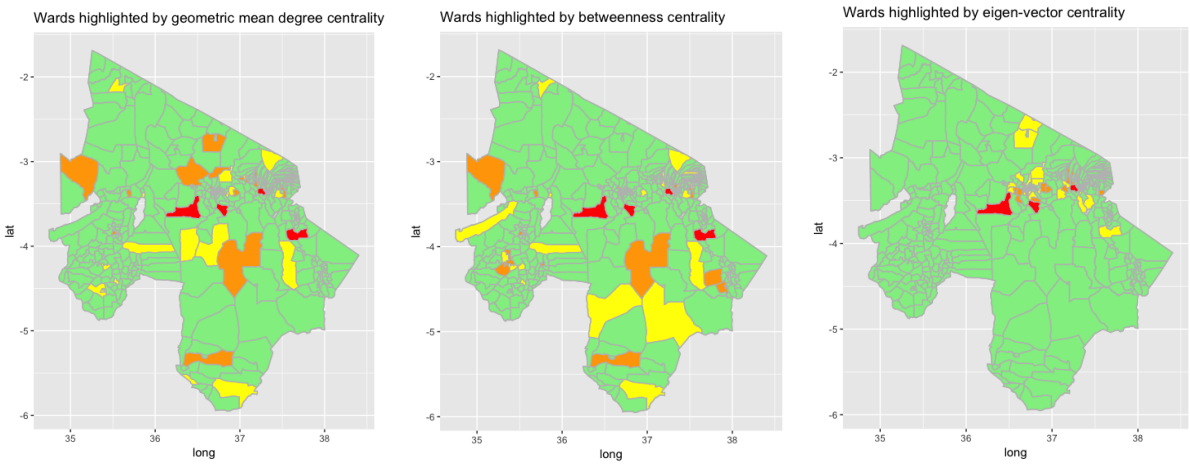

Figure 1. Spatial distribution of wards with highest centrality measures in the northern Tanzania livestock movement network, colour shows position in each centrality measure rank, out of 398: red, top 1%; orange, 1-5%; yellow, 5-10%.

Simulated movements and pathogen transmission

Mean reductions in population cumulative incidence (PCI) after 1 year for the fast and slow pathogens for each intervention scenario are shown in Figure 2. Reductions are relative to PCI reached after 1 year with no intervention (fast: 24%; slow: 1.7%). The higher the reduction in PCI, the more effective the intervention. The list of trialled interventions and associated PCI are given in Tables S3 and S4. All simulated interventions had greater reduction in PCI for the fast pathogen example compared to the slow, although the ranking of intervention efficacy was similar for both fast and slow pathogens. The movement ban implemented in all 111 market wards (high economic and logistical costs) performed only slightly better than when targeted in only 20 wards using network measures, and network-based targeting was more effective than selecting wards using population size or randomly, although there was no substantial difference in performance between the network measures. Vaccination applied to all wards achieved a 100% reduction in PCI for both fast and slow pathogens, while the best-performing targeted intervention, degree centrality, achieved reductions in PCI of 58% (fast) and 31% (slow). The "common sense" intervention of targeting using the total number of cattle performed almost as well as degree centrality, and similarly to the second-best network measure, betweenness, but was much less efficient, requiring 3.5 × more vaccine doses than degree centrality. Targeting vaccination using

405 eigenvalue centrality performed relatively poorly, particularly against the slow disease, where its
406 performance was comparable to selecting wards randomly.
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408
409
410
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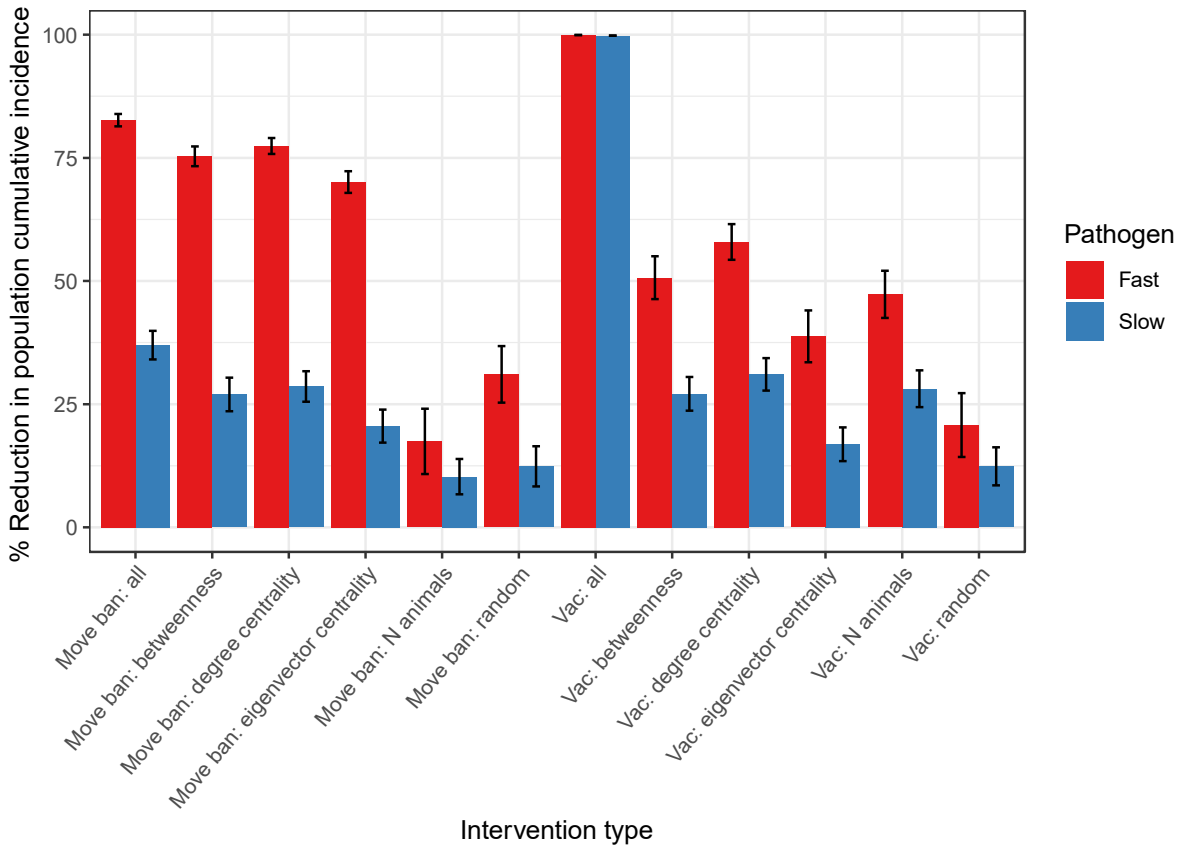

Figure 2. Mean (± SE) percentage reduction in population cumulative incidence (PCI) after 1 year for simulated 'fast' and 'slow' transmitting pathogens on the northern Tanzania cattle multiplex network for two types of intervention (market movement ban or vaccination at 70% coverage) applied using six strategies: applied to all wards; targeted to 5% (n = 20) of wards using each of three network centrality measures (betweenness, degree, and eigenvector centrality); targeted to the 5% of wards with the highest cattle population size; and applied to 5% of wards selected randomly. The greater the reduction in PCI, the more effective the intervention is at reducing total number of cases. Mean PCI under each scenario is calculated as the geometric mean of 237 simulated epidemics (full data: Tables S3 and S4).

Discussion

It is well established that the network analysis of livestock movements can be used to better understand and control diseases of commercial and zoonotic importance in higher income countries where livestock industries tend to be highly structured and movement data are centrally collected and digitised. It is less

clear that such approaches are valuable in lower income countries, where movement data are typically unavailable and the cost-benefit ratio less compelling. By exploiting movement permit data collected for health certification and tariff purposes, we have shown that even highly fragmented information about movement patterns can be used to infer network structure. By simulation, we show that the resultant inferred network has the potential to advance strategic understanding. These simulations corroborate that simple network measures can be used to identify good targets for surveillance and disease control that would be appropriate for a range of diseases and reduce the impact of infectious disease at considerably reduced cost and effort. These results could be used to form simple and practical guidelines that could be exploited immediately if, for example, a movement ban was initiated and government needed guidance on where their limited re-enforcement resources should be targeted, although they should not be used for more specific predictions without further data and analysis. They also provide a foundation for deeper research effort, highlighting where the collection of additional empirical data would be useful. For example, the substantial changes in network metrics that result when spatial spread between wards is incorporated highlight the need to augment movement data with more extensive information about local patterns of contact. The homogeneous mixing assumption used at the within-ward level has previously been shown to be useful for developing strategic understanding, even in highly spatially driven scenarios [160], but more detailed recommendations would require modelling of within-ward heterogeneity supported by higher resolution data. This assumption may be less realistic for small urban wards where cattle are tethered, though in larger pastoral and agro-pastoral wards, shared natural resource points might make homogeneous mixing more appropriate (G.L.C., unpublished data and [158]). Similarly, while the assumption that cattle-to-market movements occur from adjacent wards is consistent with two authors' expert knowledge of livestock management practice (O.M.N. and E.S.), verification with further data collection is an important next step. Finally, simulated movements are dynamically generated based on the random variation generated within the stochastic simulation models. We have not investigated in our dataset evidence of dynamic patterns such as changing network patterns over time because the patchy missingness in our data limits the complexity of the movement model. If more complete data became available for analysis it would be beneficial to assess the evidence for link rewiring throughout the year as this could indicate where control measures

should be targeted at specific times. Further potential model deficits include the similar impact of targeting control measures when comparing across centrality measures. This may in part because of the relative crudeness of the disease model; in a more sophisticated model, where the timescales and frequencies of links were considered in greater detail, more substantial differences might be apparent. Similarly, a more explicit model of spatial spread might also prove discriminatory. Finally, the addition of pathogen sequence data where these are available, would provide valuable confirmation of the role of network structure.

Conclusions

Despite this demonstration of the value of our inferred network approach, we note that data generation was the result of substantial, time consuming effort, and the resultant inferred network, while useful, has limitations as noted above. Mobile broadband technology is becoming increasingly accessible and coupled with the availability of inexpensive scanning devices, the adoption of routine, robust digitised data recording should be achievable. In this paper, we have shown the benefits of having this data to be potentially substantial. This will be particular pertinent in emerging economies such as Tanzania, where changes in industry structure are likely to have unanticipated disease impacts and will require regular monitoring.

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